

TRANSFER OF SOME SPECIES FROM *GILIA* TO *ALLOPHYLLUM* AND
TINTINABULUM, AND THE EFFECTS OF THE TRANSFER ON THE GENERIC
DEFINITION OF *GILIA* (POLEMONIACEAE)

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ABSTRACT

Three species of *Gilia* are transferred to *Allophyllum* and one to *Tintinabulum*. The transfers are supported by pollen morphology as well as by type of vestiture and various gross morphological characters. *Allophyllum* now has an expanded range of variation with two sections, *Allophyllum* sect. *Allophyllum* and *A.* sect. *Kelloggia*, *comb. nov.* The small genus *Tintinabulum* now has four species including *T. tenerimum*, *comb. nov.* The exclusions make *Gilia* more natural than it has been in many decades. The tribe Gilieae has also become more natural or monophyletic as a result of the present and other recent transfers. Pollen aperture arrangement turns out to be a very good taxonomic character in the Polemoniaceae. The *Gilia* tribe is zonocolporate with rare exceptions, while the other tribes with rare exceptions are pantoporate. The approach of molecular cladistics to classification of Polemoniaceae is critiqued.

KEY WORDS: *Gilia*, *Allophyllum*, *Tintinabulum*, *Aliciella*, Polemoniaceae, pollen morphology, phylogeny

This paper deals with the relationships of four species of western montane annual herbs which have long been treated as members of *Gilia*. Three of the species--*G. leptalea* (A. Gray) Greene, *G. capillaris* Kellogg, and *G. sinistra* M.E. Jones--currently form the section *Kelloggia* of *Gilia* (Day 1993a, 1993b; Grant 1999). The fourth species is the *G. tenerima* A. Gray of floras and manuals.

On external morphology, the four species appear to belong in *Gilia*. However, certain microscopic characters have forced a reconsideration of their relationships. In pollen characters, section *Kelloggia* differs from the rest of *Gilia*, but agrees with *Allophyllum*. The four species possess a type of glandular hair that is found in *Allophyllum* and *Tintinabulum*, but not in the rest of *Gilia*. There are also some gross morphological characters that differentiate the four species from *Gilia* proper.

The character relationships suggest that the four species should be taken out of *Gilia*, that section *Kelloggia* should be placed in *Allophyllum*, and that *G. tenerrima* A. Gray belongs in *Tintinabulum*. Here we present the evidence for the proposed transfers and make the formal taxonomic and nomenclatural changes. The effects of the changes on the definition of the genera *Allophyllum* and *Gilia* and the tribe Gilieae are discussed.

We will sometimes refer to the species involved as gilies, sometimes as allophyllums or tintinabulum, depending on the historical context. When referring to a given species as it was in the past, we cite it as a *Gilia*, but it is cited as an *Allophyllum* or *Tintinabulum* when looking to the future. The term "true gilies" is used for the genus *Gilia* exclusive of section *Kelloggia* and *G. tenerrima* A. Gray. The original members of *Allophyllum* will be referred to as the "typical allophyllums" or *Allophyllum* sect. *Allophyllum*.

CHARACTERS

Pollen morphology.

Good surveys of the various morphological features of the pollen grains in the family Polemoniaceae as a whole were made by Stuchlik (1967a, 1967b) and Taylor & Levin (1975). Additional observations in particular genera have been recorded for *Collomia*, *Acanthogilia*, and *Maculigilia* (Chuang *et al.* 1978; Day & Moran 1986; Patterson 1989). *Maculigilia* is a new monotypic genus recently segregated from *Gilia* (Grant 1999). Day investigated pollen morphology in *Gilia* proper, *G. tenerrima* A. Gray, and *Allophyllum*, and the new results are presented here (Table 1, Figure 1).

Because there are numerous palynological characters varying among numerous polemon genera and species, authors have sought to reduce this variation to a manageable number of syndromes or "types" (Stuchlik 1967a, 1967b; Taylor & Levin 1975; Chuang *et al.* 1978). This has its advantages, but also disadvantages. Important single characters become lost in the aggregate syndrome.

The location of the apertures on the pollen grain is one such character. We have singled it out and found it to be a very useful indicator of relationships. Two contrasting conditions are: pantoporate (apertures scattered over grain) and zonocolporate (apertures located in the equatorial zone).

In all sections of the true gilies, the pollen is zonocolporate. In the original or typical allophyllums, by contrast, it is pantoporate. In the three species of section *Kelloggia*, it is also pantoporate (Table 1, Figure 1).

Table 1. Several characters of the pollen grains (pore location and exine pattern) in typical *Allophyllum* and some former members of *Gilia*. From Stuchlik (1967a), Taylor & Levin (1975), and Day (herein).

- Allophyllum gilioides* (Bentham) A.D. Grant & V. Grant. Pantoporate; perpectate, spinulose. California. *Ellison, s.n.* (Stuchlik).
- A. gilioides* (Bentham) A.D. Grant & V. Grant subsp. *gilioides*. Pantoporate; perpectate, spinulose. California. *Hoover 3003*. (Taylor & Levin).
- A. gilioides* (Bentham) A.D. Grant & V. Grant subsp. *violaceum* (Heller) A.G. Day. Pantoporate; perpectate, spinulose. Lake Almanor, Plumas Co., CA. *Taylor 4639*. (Day).
- A. divaricatum* (Nuttall) A.D. Grant & V. Grant. Pantoporate; perpectate, spinulose. Twain Harte, Tuolumne Co., CA. *V. Grant & A.D. Grant 9449*. Figure 1A. (Day).
- Gilia sinistra* M.E. Jones subsp. *sinistra*. Pantoporate; perpectate, spinulose. Blue Mts., Asotin Co, WA. *Cronquist 5915*. Originally reported as *G. capillaris* Kellogg, but specimen reidentified as above. (Stuchlik).
- G. sinistra* M.E. Jones subsp. *sinistra*. Pantoporate, perpectate, spinulose. Sagehen Creek, Nevada Co., CA. *Day & Trewbridge 83-74*. Figure 1B. (Day).
- G. sinistra* M.E. Jones subsp. *pinnatisecta* (Mason & A. Grant) Day. Weaverville, Trinity Co., CA. *Day & Robinson 84-19*. (Day).
- G. capillaris* Kellogg. Pantoporate; striate. Holcomb Valley, San Bernardino Mts., s. CA. *A.G. Day 62-20*. (Day).
- G. leptalea* (A. Gray) Greene subsp. *leptalea*. Pantoporate; striate. Butte Meadows, Butte Co., CA. *Heller 12817*. (Taylor & Levin). Note: the authors report zonocolporate pollen in their description, but their photograph shows it to be pantoporate.
- G. leptalea* (A. Gray) Greene subsp. *bicolor* Mason & A.D. Grant. Pantoporate; striate. Sagehen Creek, Nevada Co., CA. A.G. Day 82-100. Figure 1C. (Day).
- G. leptalea* subsp. *bicolor*. Pantoporate; striate. Slate Creek Valley, Mono Co., CA. *Clausen 1962*. (Day).
- G. filiformis* Parry ex A. Gray. Zonocolporate; striate. California. *Craig 843*. (Stuchlik).
- G. tenerrima* A. Gray. Zonocolporate, with numerous closely-spaced colpi, \pm equatorial in position, but the equatorial band sometimes modified into a figure-of-8 form; exine striate. Bodie Hills near Masonic Mt., Mono Co., CA. *Lavin SW31b*. (Day).

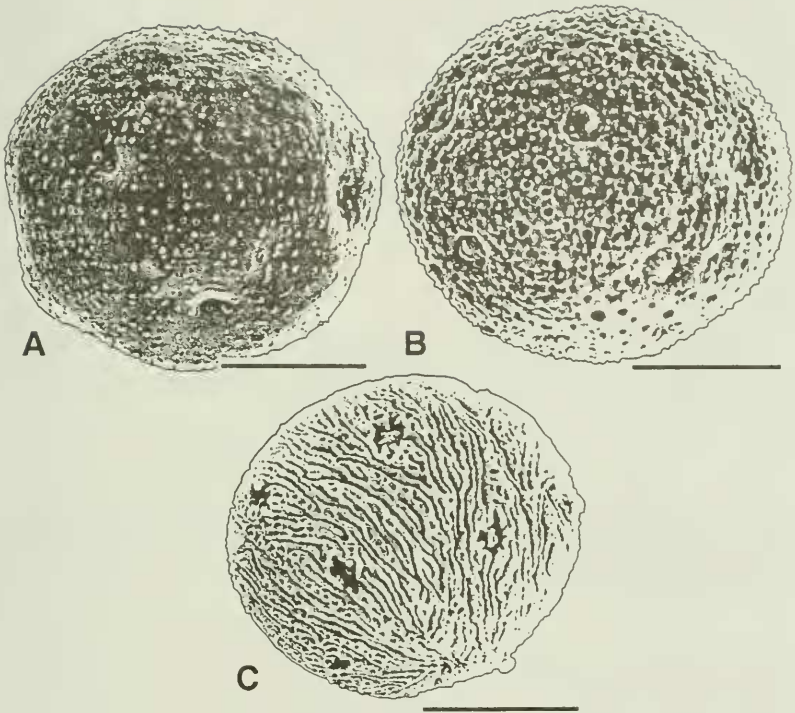


Figure 1. Pollen grains of *Allophyllum* and *Gilia* sect. *Kelloggia*. (A) *Allophyllum divaricatum* (Nuttall) A. Grant & V. Grant; Twaine Harte, Tuolumne Co., CA. (B) *Gilia sinistra* M.E. Jones ssp. *sinistra*; Sagehen Creek, Nevada Co., CA. (C) *Gilia leptalea* (Gray) Greene ssp. *bicolor* Mason & A. Grant, Slate Creek Valley, Mono Co., CA. Collection numbers in Table 1. Drawn from SEM photos of Day. Scale line 15 microns.

Next, consider the exine pattern. In *Gilia* exclusive of *Kelloggia*, the pattern varies but is commonly striate. In *Allophyllum* sect. *Allophyllum*, the exine has spinules. *Gilia sinistra* has a spinulose exine like typical *Allophyllum*. However, the exine is striate in *Gilia capillaris* and *G. leptalea* (Table 1, Figure 1). Thus, the exine pattern varies among species in *Kelloggia*, but exhibits the typical *Allophyllum* condition in one of the species.

Gilia tenerrima has zonocolporate striate pollen, as does *G. filiformis* Parry ex A. Gray (Table 1). The pore arrangement in *G. tenerrima* is unusual, which led to its being misinterpreted as "approaching pantoporate" in a previous paper (Grant 1999). A better characterization is broad-banded zonocolporate (see Table 1).

Trichomes.

The true *gilia*s and *Allophyllum* sect. *Allophyllum* both have stipitate glandular hairs on the upper stems and often in the inflorescence. These trichomes consist of a chain-like series of cells forming a stalk and a terminal globular single-celled sticky gland. In the species of true *gilia*s that have been examined, the stalk is generally stout and the terminal gland is usually amber-colored. In typical *Allophyllum*, the stalk is long, slender, and translucent, and the terminal gland is a black dot (Figure 2).

The latter type of glandular hair is unusual in the temperate genera, but is found again in a modified form in *Kelloggia*. The glandular hairs of *Kelloggia* are greatly reduced in size as compared with typical *Allophyllum*. They often have a short single-celled stalk, in which case they measure ca. 0.05 mm long. The terminal gland is a black dot as in typical *Allophyllum* (Figure 2).

The glandular hairs of *Gilia tenerrima* are also of the *Allophyllum* type, with a slender hyaline stalk bearing a black dot-like gland. They are tiny as in *Kelloggia*, measuring 0.07-0.13 mm long. We at first construed this as evidence for a relationship of *G. tenerrima* with *Allophyllum* sect. *Kelloggia*, but then we discovered the same type of tiny black-tipped gland in *Tintinabulum inyoensis* (I.M. Johnston) V. Grant, which *G. tenerrima* resembles in gross morphological characters.

Other Characters.

Seed form and color are conservative characters in the temperate Polemoniaceae, and are good indicators of generic and tribal relationships (Grant 1998). The true *gilia*s and *Allophyllum* sect. *Allophyllum* differ with respect to these seed characters. In true *gilia*s, the seeds are small, angular, and sandy colored. In typical *Allophyllum*, they are large, plump, with a rounded contour on one side at least, and brown or black. It is significant that mature seeds of *Kelloggia* are also plump, rounded and dark brown, as in typical *Allophyllum*.

To summarize, the three species of *Kelloggia* differ from the rest of *Gilia*, but agree with *Allophyllum* sect. *Allophyllum* in pollen pore arrangement, type of trichome, and seed characters. In addition, one species of *Kelloggia* is like the typical *allophyllum*s in pollen exine pattern.

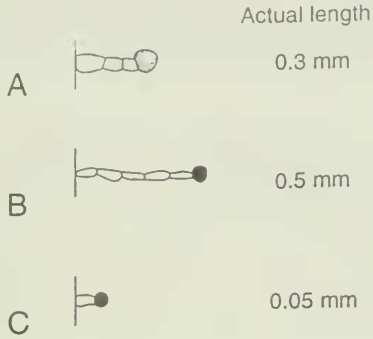


Figure 2. Types of stipitate glandular hairs. Hairs shown as attached to side of upper stem or pedicel. The terminal gland is amber-colored in A, and black in B and C. (A) *Gilia capitata* Sims ssp. *pacifica* V. Grant; Mendocino Co. coast. (B) *Allophyllum violaceum* (Heller) A. Grant and V. Grant; southern Sierra Nevada, Kern Co. (C) *Gilia leptalea* (Gray) Greene; central Sierra Nevada, Sierra Co. All localities in California. A and B to same scale, C drawn at a much higher magnification than A and B.

Gilia tenerrima has a growth habit of spreading branches with slender stems, and the flowers are usually solitary. In these respects it differs from *Gilia* proper but is like *Tintinabulum*. The corolla is small and campanulate in both *G. tenerrima* and *Tintinabulum*. As noted earlier, tiny black-tipped glandular hairs occur in both *G. tenerrima* and *Tintinabulum inyoensis*.

The DNA evidence published to date for *Kelloggia* is scanty. It consists of the sequence in the cpDNA gene matK in *Gilia sinistra* (Johnson *et al.* 1996). In the cladogram for this gene, *G. sinistra* falls in a clade of *Navarretia* species (Johnson *et al.* 1996). *Gilia sinistra* is remote from *Navarretia* by nonmolecular criteria of relationships. More molecular work on *Kelloggia* is desirable.

In the cpDNA and nrDNA cladograms (Johnson *et al.* 1996; Porter 1997), *Gilia tenerrima* falls close to the far-western annual gilies (*Gilia* subgen. *Gilia*), but is remote from *G. filiformis*. This is one of the unexplained cases of discordance between molecular and morphological data in the family.

THE EXPANDED GENUS *ALLOPHYLLUM*

Allophyllum is a small genus related to *Collomia* in the tribe Polemonieae. It was set up in 1955 for the former *Gilia gilioides* (Bentham) Greene group (Grant & Grant 1955). The group consists of four or five species depending on how one treats the taxa *gilioides* and *violaceum*. These entities behave as distinct sympatric species in some parts of their range (Grant & Grant 1955) and as intergrading races in other areas (Day 1993b, unpubl.). Accordingly, one can treat them either as separate species (Grant & Grant 1955) or as two subspecies of one species (Day 1993a, 1993b). We will treat them as one polytypic species in this paper.

The transfer of the *Gilia leptalea* group to *Allophyllum* introduces a distinctive element into the genus and expands its range of variation. The relationships between the old *allophyllums* and the new *A. leptaleum* (A. Gray) A. Day & V. Grant group can be expressed taxonomically by treating them as separate sections.

The revised classification of *Allophyllum* is presented in outline form. Diagnoses are given rather than descriptions. The essential nomenclature is presented rather than complete synonymy. For more details see the treatments of Grant & Grant (1955) and Day (1993a).

ALLOPHYLLUM (Nuttall) A. Grant & V. Grant, *Aliso* 3:98. 1955. TYPE SPECIES: *Gilia divaricata* Nuttall. BASIONYM: *Gilia* sect. *Allophyllum* Nuttall, *J. Acad. Nat. Sci. Philadelphia*, ser. 2 1:155. 1848.

Annual herbs with leafy stems. Plants medium-sized to small. Leaves digitately lobed or simple and entire. Pubescence of glandular hairs consisting of slender translucent stalks and small black tips. Calyx with herbaceous lobes and membranous sinuses. Corolla funnelform, medium-sized to small. Pollen pantoporate. Capsule

spherical, dehiscent from top to bottom, and the valves generally falling off. Seeds plump, rounded on one side, brown or black, mucilaginous when wet. Basic chromosome numbers $X = 9, 8$.

Western North America, mainly in the Pacific states, but extending into interior western states. Seven (or eight) species in two sections.

ALLOPHYLLUM sect. *ALLOPHYLLUM*

Leaves digitately lobed with an elliptical terminal lobe and 2-5 smaller lateral lobes; tips of lobes blunt and thickened. Glandular hairs relatively large in comparison with section *Kelloggia*. Flowers generally in clusters. Corolla generally concolored. Pollen exine spinulose. Seeds black or brown. Basic chromosome numbers, $X = 9, 8$.

Allophyllum divaricatum (Nuttall) A. Grant & V. Grant, *A. integrifolium* (Brand) A. Grant & V. Grant, *A. glutinosum* (Benth.) A. Grant & V. Grant, *A. gilioides* (Benth.) A. Grant & V. Grant subsp. *gilioides*, and *A. gilioides* subsp. *violaceum* (Heller) A.G. Day. Mostly at lower and middle elevations but ranging to higher elevations in mountains.

ALLOPHYLLUM sect. *KELLOGGIA* (Mason & A. Grant) A. Day & V. Grant, *comb. nov.* TYPE SPECIES: *Gilia capillaris* Kellogg. BASIONYM: *Gilia* subgen. *Kelloggia* Mason & A. Grant, Madroño 9:219. 1948. *Gilia* sect. *Kelloggia* A. Day, Novon 3:332. 1993.

Leaves mostly linear and unlobed, sometimes bilobed in *Allophyllum sinistrum* (M.E. Jones) A. Day & V. Grant; leaf tips sharp-pointed in *A. leptaleum* (A. Gray) A. Day & V. Grant and *A. capillare* (Kellogg) A. Day & V. Grant, but blunt in *A. sinistrum*. Glandular hairs tiny compared with those in section *Allophyllum*. Flowers solitary in upper leaf axils. Corolla concolored, bicolored or tricolored, showy or small. Pollen exine spinulose in *A. sinistrum*, but striate in the other two species. Seeds dark brown at maturity. Basic chromosome number, $X = 9$.

Three species as listed below.

1. *Allophyllum capillare* (Kellogg) A. Day & V. Grant, *comb. nov.* BASIONYM: *Gilia capillaris* Kellogg, Proc. California Acad. Sci. 5:46. 1873.

Mountains from southern Oregon to southern California, east to Idaho; rare in Utah. Occurs sympatrically with *Allophyllum sinistrum*.

2. *Allophyllum leptaleum* (A. Gray) A. Day & V. Grant, *comb. nov.* BASIONYM: *Collomia leptalea* A. Gray, Proc. Amer. Acad. Arts 8:261. 1870. *Gilia leptalea* Greene, Erythea 4:58. 1896.

Cascade Mountains of Oregon to southern Sierra Nevada of California.

- 2a. *Allophyllum leptaleum* (A. Gray) A. Day & V. Grant subsp. *leptaleum*.

Wide ranging.

- 2b. *Allophyllum leptaleum* (A. Gray) A. Day & V. Grant subsp. *bicolor* (Mason & A. Grant) A. Day & V. Grant, *comb. nov.* BASIONYM: *Gilia leptalea* (A. Gray) Greene subsp. *bicolor* Mason & A. Grant, *Madroño* 9:220. 1948.

High Sierra Nevada in Mono County, California.

3. *Allophyllum sinistrum* (M.E. Jones) A. Day & V. Grant, *comb. nov.* BASIONYM: *Gilia sinistra* M.E. Jones, *Contrib. West. Bot.* 10:57. 1902.

Mountains from southern Washington to southern California, east to Nevada; rare in Colorado.

- 3a. *Allophyllum sinistrum* (M.E. Jones) A. Day & V. Grant subsp. *sinistrum*.

Wide ranging.

- 3b. *Allophyllum sinistrum* (M.E. Jones) A. Day & V. Grant subsp. *pinnatisectum* (Mason & A. Grant) A. Day & V. Grant, *comb. nov.* BASIONYM: *Gilia leptalea* (A. Gray) Greene subsp. *pinnatisecta* Mason & A. Grant, *Madroño* 9:220. 1948. *Gilia sinistra* M.E. Jones subsp. *pinnatisecta* A. Day, *Novon* 3(4):332. 1993.

North Coast Ranges, California.

TINTINABULUM TENERRIMUM

In a previous paper (Grant 1999), a small species group consisting of *Gilia campanulata* A. Gray, *G. filiformis* Parry ex A. Gray, and *G. inyoensis* I.M. Johnston was excluded from *Gilia*. The long dormant genus *Tintinabulum* of Rydberg (1917) was revived to accommodate them. A modern characterization of *Tintinabulum* has been given recently (Grant 1999) and does not need to be repeated here. *Tintinabulum* was assigned to the tribe Gilieae.

In the same paper (Grant 1999), *Gilia tenerrima* A. Gray was transferred to *Allophyllum*. This change was based on the finding of several *Allophyllum*-like characters in *G. tenerrima*: namely, rounded brown seeds, tiny black-tipped glands, a type of leaf lobing and capsule dehiscence, and what was thought to be semi-pantoporate pollen. Since then it has been found that the pollen of *G. tenerrima* is atypical zonocolporate (Table 1) and that tiny black-tipped glands occur in *Tintinabulum inyoensis* (I.M. Johnston) V. Grant as well as in *Allophyllum*. These findings weaken the case for an *Allophyllum* relationship.

Gilia tenerrima shares a number of distinctive vegetative and floral characters in common with *Tintinabulum*: spreading growth habit, slender stems, solitary flowers, campanulate corollas. These character similarities indicate a relationship. *Gilia tenerrima* was grouped with the *G. campanulata* alliance in two previous treatments (Mason & Grant 1951; Day 1993a), and, after a brief stay in *Allophyllum*, is now returned to that alliance.

Tintinabulum tenerrimum (A. Gray) A. Day & V. Grant, *comb. nov.*
BASIONYM: *Gilia tenerrima* A. Gray, Proc. Amer. Acad. Arts 8:277. 1870.
Navarretia tenerrima Kuntze, Rev. Gen. Pl. 2:433. 1891. *Allophyllum tenerrimum* V. Grant, Phytologia 84:79. (1998) 1999.

DISCUSSION

Progress in the Delineation of *Gilia*

At the turn of the last century the genus *Gilia* was a collection of distantly related subgroups, many of which were closer to other genera than they were to the core sections of *Gilia*. The genus was highly polyphyletic. The genus problem facing botanists was to identify the monophyletic subgroups that were contributing to the polyphyly of *Gilia* and to segregate them out into other genera.

The process of moving unrelated subgroups out of *Gilia* was begun early in the 20th century by Milliken (1904), who set up the segregate genus *Navarretia*, and transferred *Gilia maculata* Parish to *Linanthus*. The process was continued by a succession of later botanists. By the time of the general treatment of *Gilia* of Grant (1959), most of the large extraneous subgroups had been placed elsewhere in the system, and *Gilia* had become a fairly natural genus.

But some extraneous species and small species groups still remained in *Gilia* in 1959. Moran (1977) transferred *Gilia uncialis* Brandege to *Linanthus*. More recently, Grant (1999) excluded *G. tenerrima* A. Gray from *Gilia*, and moved the small *G. campanulata* A. Gray group into the resurrected genus *Tintinabulum*. The transfer here of the *G. leptalea* (A. Gray) Greene group to *Allophyllum* is in line with the earlier moves. It is interesting that no transfers from other genera into *Gilia* have been made in modern times.

Gilia is now more natural than it has been in the past. A putative phylogenetic tree of the genus based on all available taxonomic characters, conventional and unconventional, is shown in Figure 3. The subgenera and sections of *Gilia* are linked together by shared conservative characters in seeds, pollen, and basic chromosome number, and by various less conservative characters in leaves, pubescence, calyx, and corolla (see Grant 1998, 1999).

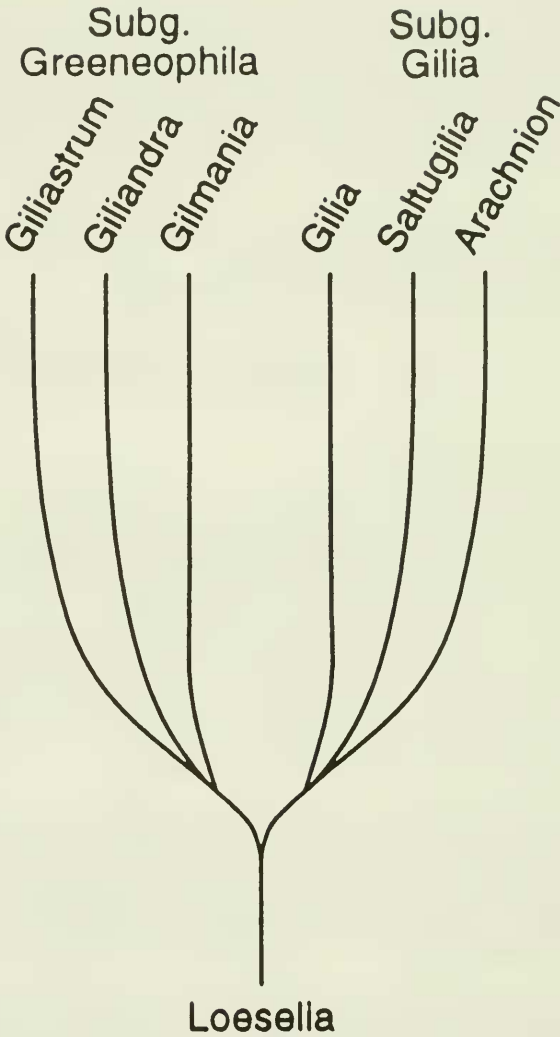


Figure 3. The subgenera and sections of Gilia after the transfers made here, and the proposed phylogenetic relationships of these subgroups.

Comments on the Segregation of the Genus *Aliciella*

The splitting off of subgroups as segregate genera can go too far. Where should we draw the line? Segregating subgroups out of a genus in order to reduce polyphyly is one thing; splitting the branches of a single monophyletic group into separate genera is something else. The first action is necessary for phylogenetic taxonomy; the latter type of change is unnecessary from a phylogenetic standpoint. Furthermore, the splitting up of a heterogenous, but monophyletic genus into two or more separate genera is generally undesirable taxonomically since it obscures the relationship between the branches.

Porter (1998a) has recently segregated the genus *Aliciella* from *Gilia* proper. *Aliciella* sensu Porter corresponds to *Gilia* sects. *Giliandra* and *Gilmania* (Figure 3; Grant 1999). In a second paper, Porter (1998b) elevates the section *Giliastrum* of *Gilia* to a separate genus. Porter's stated reason for the changes made in both papers is to reduce polyphyly in *Gilia*. Thus, Porter has the same goal as we do, but arrives at a very different result.

Porter is an exponent of molecular cladistics, whereas our work is carried out in the framework of traditional taxonomy and evolutionary systematics. The two approaches are very different, and they lead to disagreement regarding phylogenetic classification of *Gilia*. Molecular cladistics emphasizes the diagnostic value of single DNA segments, and it processes the DNA evidence by the procedures of cladistics to produce cladograms. The cladograms are often misconstrued in practice as organismic phylogenies (see Grant 1998). Traditional and evolutionary systematists have learned from long experience to beware of overemphasis on any single character; we stress the importance of using all available characters to construct classifications and infer phylogenies. The best use of DNA evidence in systematics, in our opinion, is to integrate it with all other types of evidence, rather than to overgeneralize from a molecular cladogram (Turner 1998; Grant 1998).

Porter's (1998a) segregation of *Aliciella* from *Gilia* is based primarily on the molecular cladogram for nrDNA ITS (Porter 1997). Supplementary evidence comes from Johnson *et al.*'s (1996) work on the cpDNA gene matK, but these authors assayed only three of the twenty species belonging to *Aliciella* sensu Porter. Porter (1998a) cites other lines of molecular and morphological evidence (Porter 1993; Tommerup & Porter 1996). However, the role of this supplementary evidence is difficult to assess since it is unpublished (as of this writing), one reference being a dissertation and the other a lecture abstract, and the data are not summarized in the 1998 paper. Porter (1998a) does give detailed morphological descriptions of the species; but he does not present parallel short diagnoses of the main groups involved, which would be more helpful than descriptions in revealing the morphological characters used in the classification.

In addition to setting up *Aliciella* as a genus, Porter recognizes three levels of infrageneric groups; subgenera, sections, and subsections. Each one of these groups from genus to subsection is defined in cladistic terms. Here is the definition of section *Giliandra* of *Aliciella*. "Section *Giliandra* is phylogenetically defined as the most recent common ancestor of *Aliciella pinnatifida* and *A. stenothyrsa* and all of the descendants of that ancestor." (Porter 1998a, p. 27.). Parallel definitions are given

for the other main groups. Thus, the groups are clades, or cladons in the terminology of Mayr (1995) and Brummitt (1997). The only cladograms published for the *Gilia-Aliciella* group are molecular cladograms. The separation of *Aliciella* from *Gilia* subgen. *Gilia* is in agreement with the cpDNA and nrDNA cladograms, and the subdivisions of *Aliciella* correspond with the clades and subclades in the nrDNA cladogram (Porter 1997, 1998a).

But the molecular cladograms are gene trees, not organismic phylogenies. Furthermore, they can be interpreted in different ways. The cladograms are consistent with the view that *Gilia* sect. *Giliandra* and *Gilmania* (or *Aliciella*) are only distantly related to *Gilia* subgen. *Gilia*. This agrees with the prevailing view based on morphological evidence. But it does not necessarily follow that the branches involved should be separated at the genus level. For generic segregation, more evidence and stronger arguments are needed than those presented by Porter (1998a).

In another paper, Porter (1998b) takes the first step in segregating *Gilia* sect. *Giliastrum* as a genus. This short paper makes the nomenclatural changes of the species involved; it contains little discussion and our discussion will be brief. Here again, as in the case of *Aliciella*, the main evidence is the cpDNA and nrDNA cladograms of Johnson *et al.* (1996) and Porter (1997), along with other unpublished molecular studies of Porter. It appears that another big taxonomic change is being made on a narrow data base, and without considering the difference between segregation for the sake of monophyly and splitting for the sake of homogeneity.

Improved Definition of the Tribe Gilieae

The transfer of section *Kelloggia* from *Gilia* to *Allophyllum* reduced the polyphyly in the tribe Gilieae as well as that in the genus *Gilia*. It is the latest in a series of transfers that have made the *Gilia* tribe more natural. To see this in perspective, it is necessary to go back in time. When the Gilieae was set up years ago, it consisted of seven genera in three or four groups: namely, the basal genus *Gilia*; *Ipomopsis-Eriastrum-Langloisia*; *Navarretia*; and *Leptodactylon-Linanthus* (Grant 1959, p. 258). This assemblage was believed to be phylogenetically natural at that time, according to the evidence then available, but new evidence in subsequent years brought cases of unnaturalness to light, and a series of taxa were excluded from the tribe.

The species formerly known as *Ipomopsis gloriosa* (Brandege) A. Grant was segregated into the new genus *Acanthogilia* (Day & Moran 1986), and this was placed in a tribe of its own (Grant 1998). *Leptodactylon* and *Linanthus* were removed to a new tribe Leptodactyloneae on the basis of a combination of molecular and morphological characters (Grant 1998). *Navarretia* was transferred to the tribe Polemonieae on combined molecular and morphological evidence (Grant 1998). The former *Gilia maculata* Parish was placed in a new genus (*Maculigilia*) in the Leptodactyloneae (Grant 1999). The transfer of *Gilia* sect. *Kelloggia* to *Allophyllum* in this paper continues the process.

The reduced tribe Gilieae, consisting now (in our system) of *Gilia*, *Ipomopsis*, *Eriastrum*, *Langloisia*, and the resurrected genus *Tintinabulum*, is much more natural than it was. Common characters in the seeds, calyx, leaves, and ecology help to define it. To these is added unexpectedly a pollen character.

The pollen is pantoporate in the tropical and subtropical genera of the Polemoniaceae and in the temperate tribe Leptodactyloneae (Stuchlik 1967a, 1967b; Taylor & Levin 1975; Day & Moran 1986; Day unpubl.). It is pantoporate throughout the tribe Polemoniaceae with the exception of some species of *Collomia* which have zonocolporate pollen (Stuchlik 1967a, 1967b; Taylor & Levin 1975; Chuang *et al.* 1978; Day unpubl.). By contrast, the pollen is zonocolporate throughout the tribe Gilieae as presently delimited with the exception of some pantoporate species of *Eriastrum* (Stuchlik 1967a, 1967b; Taylor & Levin 1975; Day unpubl.).

Taylor & Levin (1975) related pollen characters to phylogenetic relationships in the Polemoniaceae as these two variables were understood at that time. They suggested that the zonocolporate condition was ancestral and the pantoporate condition was derived in the family (*op. cit.*, p. 110). We have more information about pollen characters and a better system of classification today. The systematic distribution of pore arrangement as we now know it, clearly indicates that the pantoporate condition is ancestral, that the zonocolporate condition is derived, and that a zonocolporate character state is definitive of the *Gilia* tribe with only a few exceptions.

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NOTE ADDED IN PROOF

The present composition of the tribe Gilieae as outlined above needs to be qualified. The five genera listed are the extant members of the tribe. Lott *et al.* (1998) have recently discovered and described a mid-Eocene genus, *Gilisenium*, which belongs in the Gilieae and is close to *Gilia*. This important discovery shows that the tribe is much older than we and others have thought.